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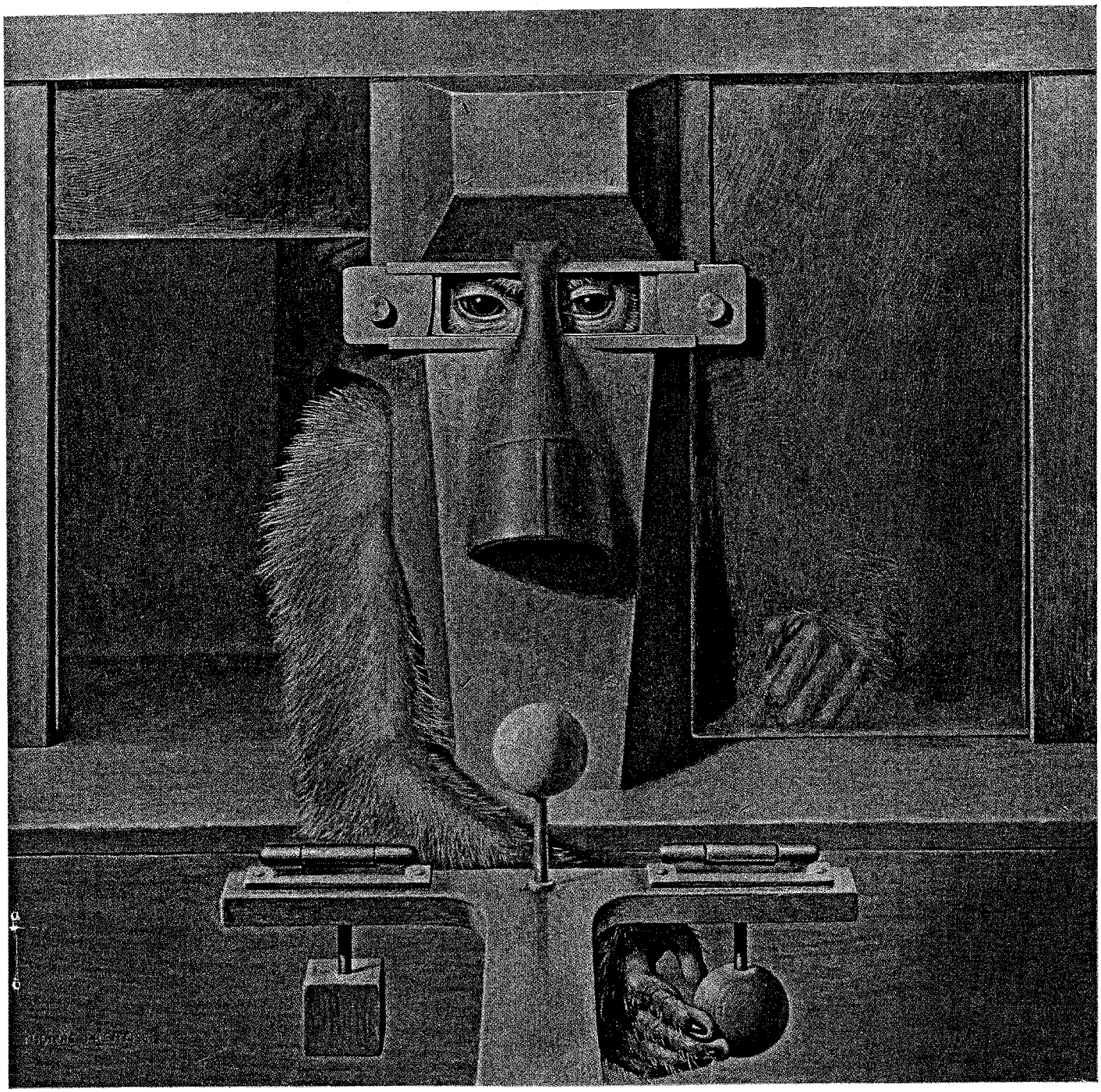

"SPLIT BRAIN" EXPERIMENT

FIFTY CENTS

January 1964

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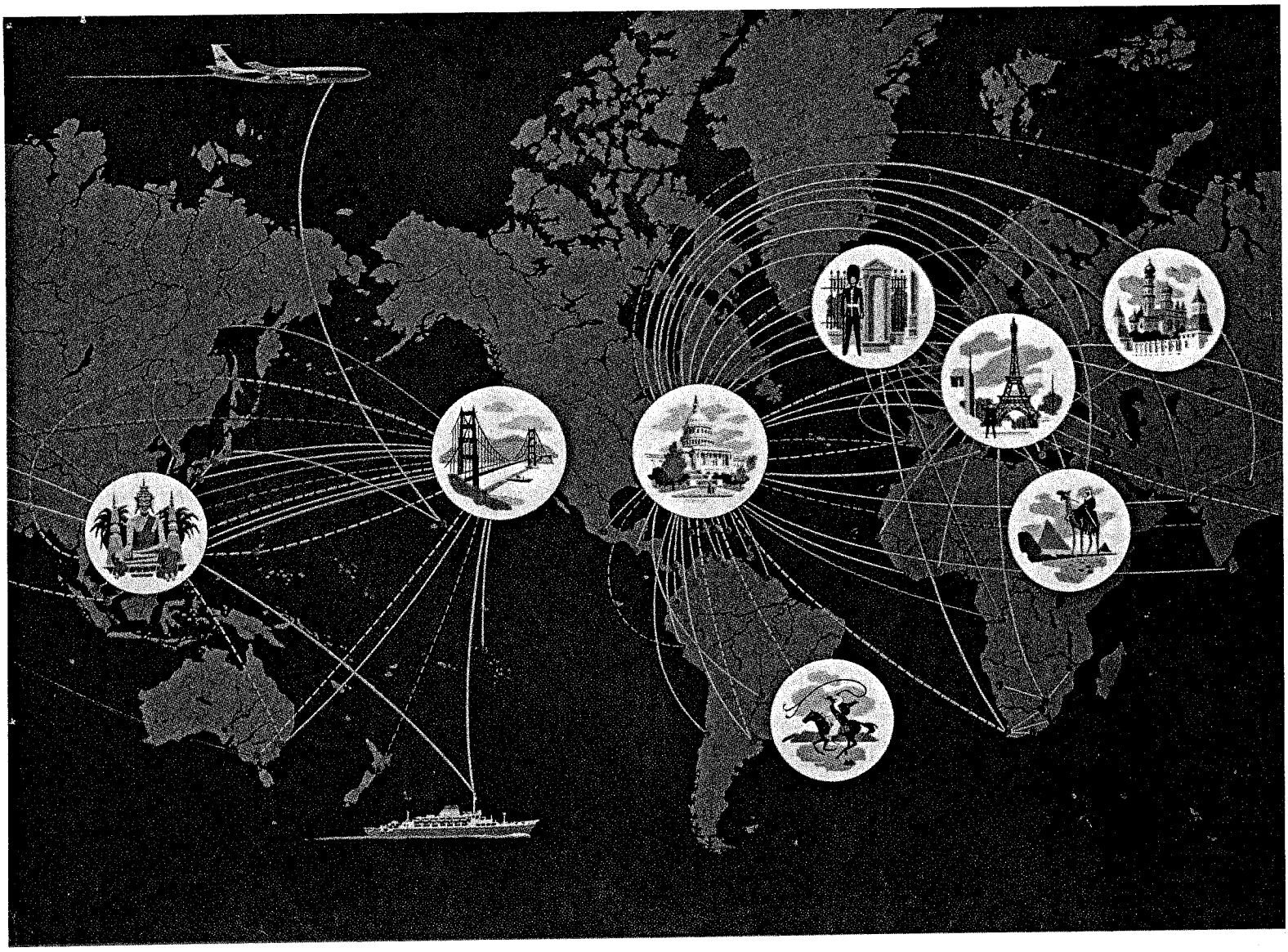

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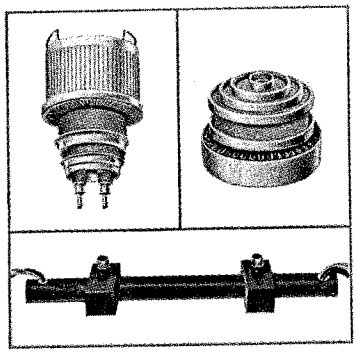

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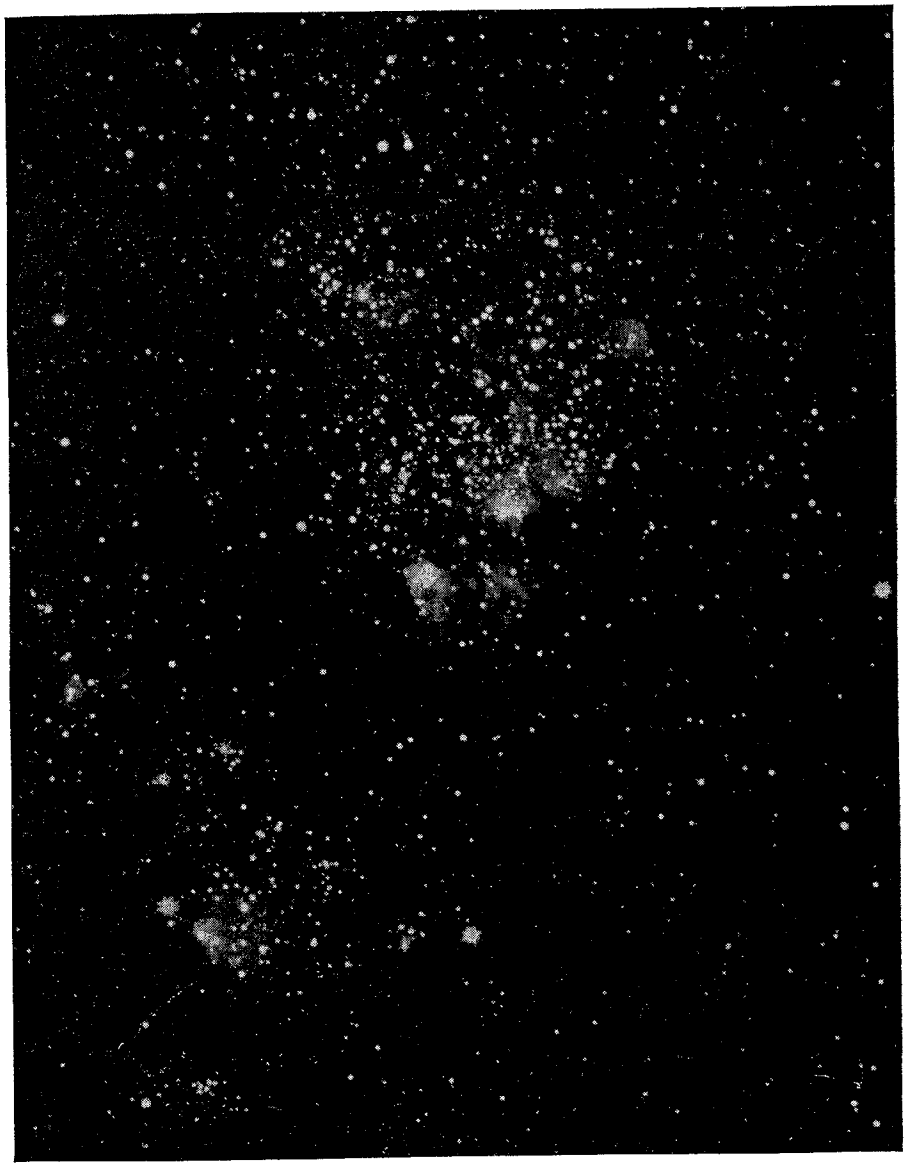
the two galaxies are the same. The spectra of stars in the Large Cloud show the same abundances of elements as the spectra of stars in our galaxy, and the abundances of elements in the Tarantula Nebula are similar to those in the Orion nebula. Detailed investigations of 50 nebulae by Helene R. Dickel, L. H. Aller and D. J. Faulkner at the Mount Stromlo Observatory and the Mount Bingar Field Station in Australia, and work on the Tarantula Nebula by Faulkner, indicate that these nebulae contain at most 30 per cent less helium and oxygen with respect to hydrogen than emission nebulae in our galaxy. On the whole the Large Cloud and our galaxy seem to be made of the same basic stuff.

When Shapley and his co-workers made a survey of the Large Cloud in 1953, they recorded for special further study a number of conspicuous assemblages of stars associated with nebulosity; to these assemblages Shapley applied the label "constellations." He had already noted that most of the brighter stars in the constellations were exceedingly blue and had vouchsafed the opinion that these were the places where stars are now being born and where the evolutionary pots are boiling fiercely. His assertions have all proved to be true, and I should like to conclude with a description of Shapley's fascinating Constellation I [*see illustration at right*].

Practically all the stars measured so far in this assemblage are exceedingly blue. The constellation is even bluer than it seems to be; it is embedded in dust that tends to redden it slightly. It probably contains no red supergiants at all. It is located near right ascension five hours 22 minutes and declination minus 68 degrees, and it can be seen quite plainly on the radio map of the Large Cloud in both 20- and 21-centimeter contours.

Constellation I appears to have a diameter of 500 light-years. Mrs. Basinski and I have estimated the total mass of its stars at about 24,000 solar masses, with an uncertainty of no more than 20 per cent. Faulkner has estimated the total mass of ionized hydrogen in it from spectra obtained at the Mount Stromlo Observatory and Mathewson has estimated this mass from radio data. With remarkable agreement, they find that the mass of ionized hydrogen is equivalent to between 50,000 and 60,000 solar masses. This is a large mass, but the mass of neutral hydrogen in the constellation is extraordinary. McGee has estimated it at five million solar masses, mostly contained within a diameter of 1,100 light-years. We thus find a few hundred stars, all formed less than 10 million years ago, located in the midst of a huge hydrogen cloud 200 times more massive than all the stars combined.

If one may ignore the unlikely hypothesis that the association of stars and gas is a chance one, the conclusion that Constellation I is expanding seems almost inescapable. On photographic plates we can see few, if any, faint or red—that is, older—stars within the confines of the grouping. If the birth of stars in the constellation is a continuing process, and if the older stars were retained by the constellation, then a minimum of 6,000 older stars should accumulate in a billion years. Obviously no such numbers are observed. The gas in the constellation can supply building material for an additional 200 generations of stars similar to the ones we see. Hence we have concluded that stars are continually being formed from the gas, presumably at a fairly steady rate, and that these stars at the time of their formation are already moving fast enough to enable them to escape from the parent cluster. A little more than five kilometers per second—nothing extravagant—would suffice. At this speed it will take a star only something of the order of 25 million years to get well beyond the limits of the constellation. The escaped stars gradually evolve to become red giants and supergiants, then intrinsically faint stars. Therefore assemblages such as Constellation I may well be the steady suppliers of ordinary stars older than 25 million years in the Large Cloud. Nowhere in our galaxy do we find the processes of star birth and evolution so neatly portrayed as they are in the Large Cloud of Magellan.



CONSTELLATION I in the Large Cloud was photographed by the author with the 74-inch reflector. These very young, extremely massive stars are embedded in a huge cloud of gas.

THE GREAT CEREBRAL COMMISSURE

This broad nerve cable and lesser bridges connect the two halves of the mammalian brain. If the connections are cut, the organism functions quite well but behaves much as though it had two brains

by R. W. Sperry

The body plan of a mammal provides for two lungs, two kidneys and paired organs such as eyes, ears and limbs. In a sense it also provides for a paired brain. In structural detail and functional capacity the two halves of the mammalian brain are mirror twins, each with a full set of centers for the sensory and motor activities of the body: vision, hearing, muscular movement and so on. Each hemisphere of the brain is mainly associated with one side of the body, the right brain presiding over the left side and the left brain over the right side. Each hemisphere's influence is not, however, always restricted in this way: when an area in one hemisphere is damaged, the corresponding area in the other often can take over its work and so control the functions involved for both sides of the body. In short, either half of the brain can to a large extent serve as a whole brain.

Anatomically, of course, the two halves of the brain are linked together and normally function as one organ. They are united not only by the common stem that descends from the brain into the spinal cord but also by a number of cross bridges between the hemispheres. Especially striking is the system of connections between the two halves of the cerebrum: the upper part of the brain. The cerebral hemispheres are linked by discrete bundles of nerve fibers, called commissures, that form reciprocal connections between parallel centers in the two hemispheres. By far the most prominent of these bridges is a broad cable known as the great cerebral commissure or, more technically, as the corpus callosum [*see illustration on pages 44 and 45*]. This massive structure, which is particularly large in primates and largest in man, contains most of the millions of nerve fibers that connect the two halves of the cerebral cortex, which is the highest integrating organ of the brain.

The size and obviously important position of the corpus callosum suggest that it must be crucial for the proper performance of the brain's functions. Many years ago, however, brain surgeons discovered to their surprise that when the corpus callosum was cut into (as it sometimes had to be for medical reasons), this severing of fiber connections between the cerebral cortices produced little or no noticeable change in the patients' capacities. The same was true in the rare cases of individuals who lacked the corpus callosum because of a congenital failure in development. Experiments in severing the corpus callosum in monkeys tended to confirm the apparent harmlessness of the operation. Accordingly in the late 1930's surgeons tried cutting the entire corpus callosum in some cases of severe epilepsy as a measure to prevent the spread of epileptic seizures from one brain hemisphere to the other. Efforts to pinpoint losses of function in this series of cases were again unsuccessful.

Exactly what purpose the corpus callosum served became more and more a mystery. In 1940 the nerve physiologist Warren S. McCulloch, then working at the Yale University School of Medicine, summarized the situation with the remark that its only proved role seemed to be "to aid in the transmission of epileptic seizures from one to the other side of the body." As recently as 1951 the psychologist Karl S. Lashley, director of the Yerkes Laboratories of Primate Biology, was still offering his own jocular surmise that the corpus callosum's purpose "must be mainly mechanical... i.e., to keep the hemispheres from sagging." The curious capacity of the brain to carry on undisturbed after the destruction of what is by far its largest central fiber system came to be cited rather widely in support of some of the more mystical views in brain theory.

Intrigued by the problem of the great cerebral commissure and the theoretical implications of this problem, my colleagues and I began an intensive investigation of the matter, starting in the early 1950's at the University of Chicago and continuing after 1954 at the California Institute of Technology. This research, carried on by many workers at Cal Tech and elsewhere, has now largely resolved the mystery of the corpus callosum; today this bundle of fibers is probably the best understood of any of the large central association systems of the brain. The investigation has gone considerably beyond the question of the corpus callosum's functions. From it has emerged a new technique for analyzing the organization and operation of the brain; this approach has already yielded much interesting information and promises to open up for detailed study many heretofore inaccessible features of brain activity.

The technique essentially consists in the study or application, in various ways, of the split brain: a brain divided surgically so that the performance of each half can be tested separately. It has entailed a series of experiments with animals, starting with cats and continuing with monkeys and chimpanzees. The findings are not confined to animals; there has also been opportunity to study human patients who had been operated on for severe epilepsy and emerged from the operation with a split brain but freed of convulsive attacks and still in possession of most of their faculties.

The split-brain studies have borne out the earlier observation that the cutting of the entire corpus callosum causes little disturbance of ordinary behavior. This is generally true even when the

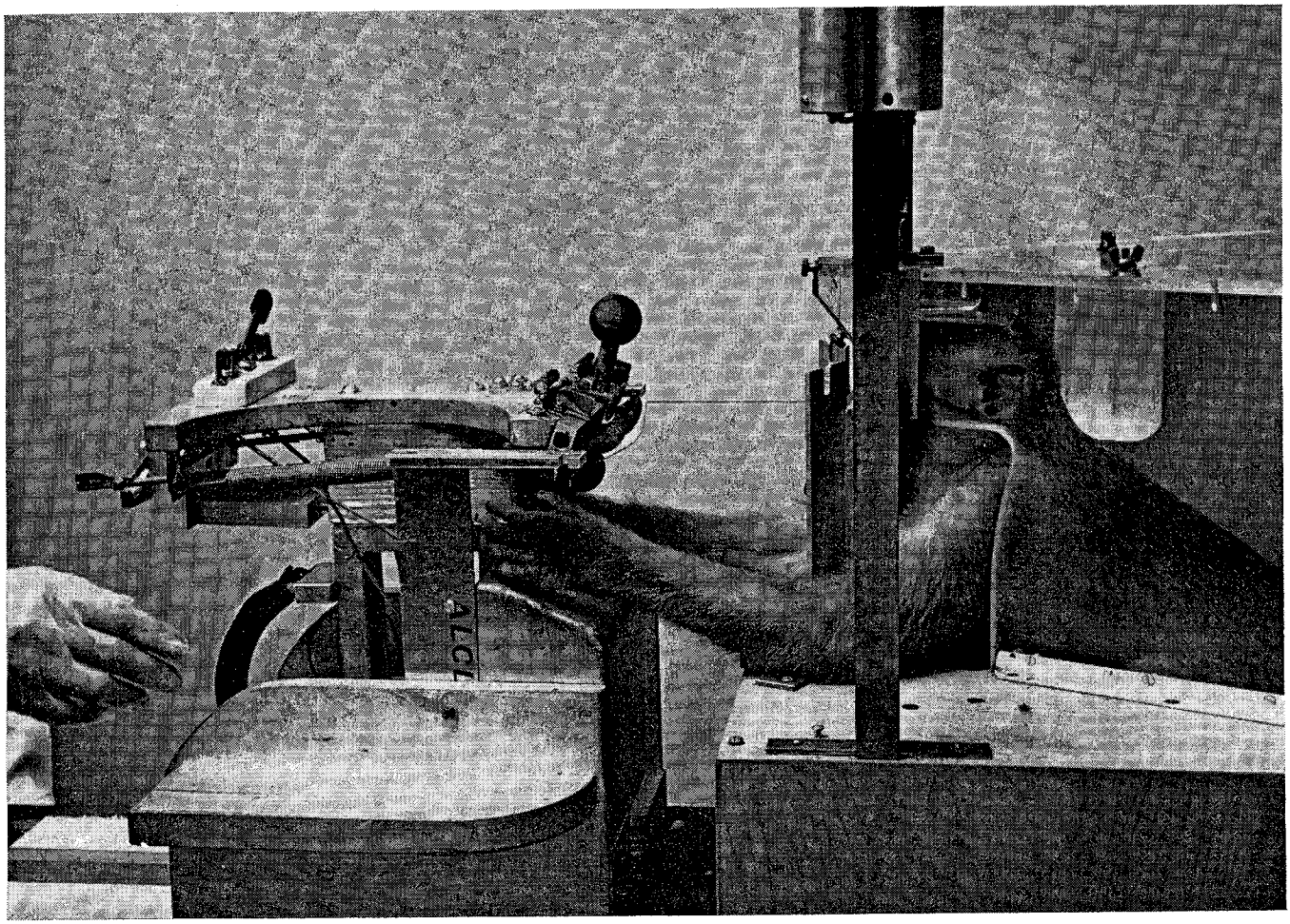
operation severs not only the corpus callosum but also all the other connections between the right and left sides of the brain down through the upper part of the brain stem. Cats and monkeys with split brains can hardly be distinguished from normal animals in most of their activities. They show no noticeable disturbance of co-ordination, maintain their internal functions, are alert and active, respond to situations in the usual manner and perform just about as well as normal animals in standard tests of learning ability. Their individual traits of personality and temperament remain the same.

It required specially designed tests to show that the split brain is not, after all, entirely normal in its function. The first convincing demonstration was provided by Ronald E. Myers, in his doctoral research started in 1951 in our laboratory at the University of Chicago and continued at Cal Tech. Testing the performance of the two brain halves separately, he found that when the corpus callosum was cut, what was learned by one side of the brain was not transferred to the other side. In fact, the two sides could learn diametrically opposed solutions to the same experimental problem, so that the animal's response in a given situation depended on which side of the brain was receiving the triggering stimulus. It was as though each hemisphere were a separate mental domain operating with complete disregard—indeed, with a complete lack of awareness—of what went on in the other. The split-brain animal behaved in the test situation as if it had two entirely separate brains.

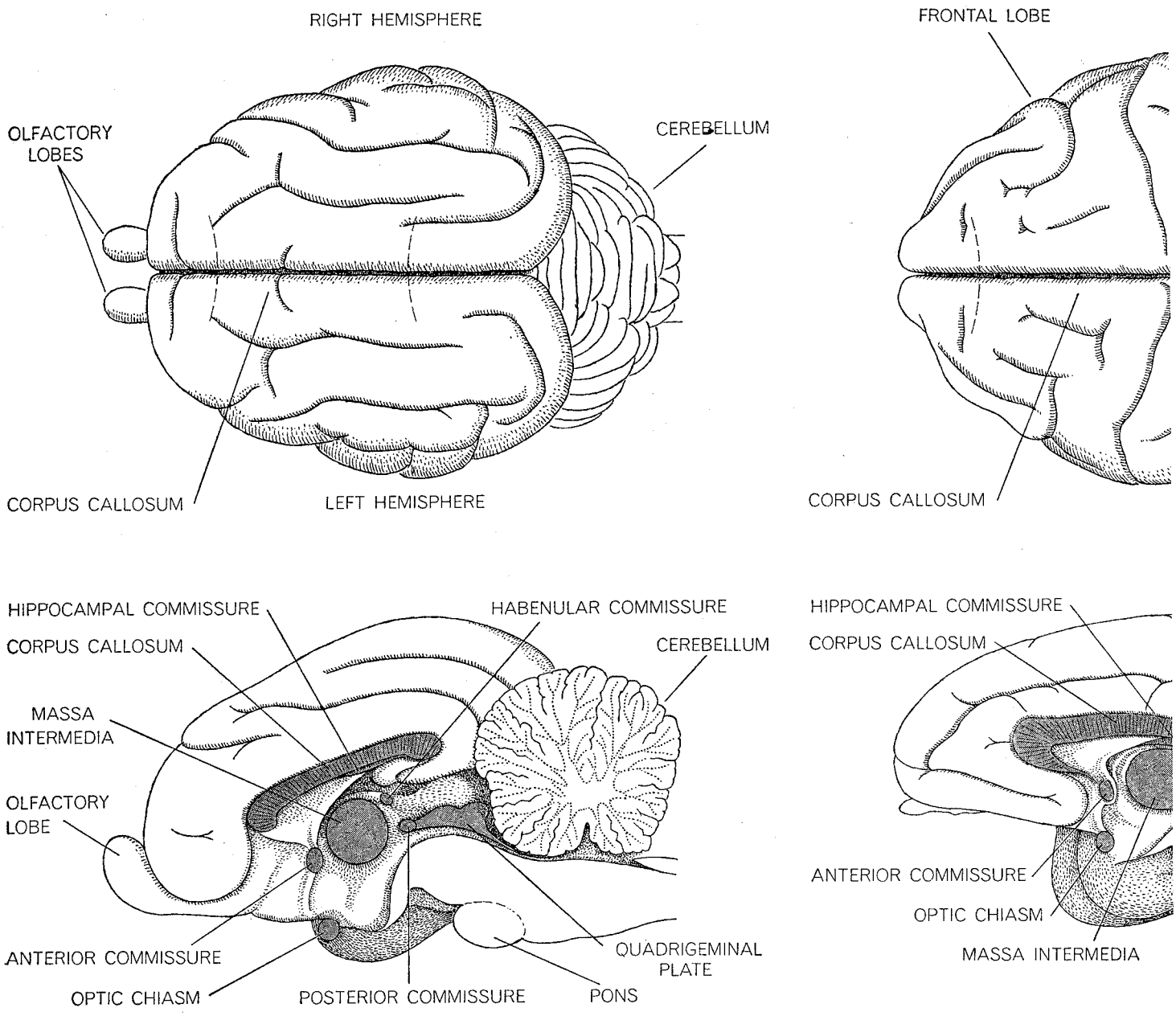
The initial experiment involved segregating each eye with half of the brain as a separate system. This was accomplishing by cutting both the corpus callosum and the structure called the optic chiasm, in which half the nerve fibers from each eye cross over to the brain hemisphere on the opposite side of the head [*see illustration on page 46*]. The effect of this combined operation is to leave each eye feeding its messages solely to the hemisphere on the same side of the head.

The animal was then trained to solve a problem presented only to one eye, the other eye being covered with a patch. The problem might be, for example, to discriminate between a square and a circle; if the animal pushed a panel bearing the correct symbol, say the square, it got a reward of food. After it had learned to make the correct choice with one hemisphere, the problem was then presented to the other eye and hemisphere, the first eye now being blindfolded. When the subject used the second eye, it reacted as if it had never been faced with the problem before. The number of trials required to relearn the problem with the second eye showed that no benefit carried over from the earlier learning with the first eye. The transfer of learning and memory from one hemisphere to the other occurred readily in animals with the corpus callosum intact but failed completely in those with the corpus callosum cut. Each hemisphere, and its associated eye, was independent of the other.

This was again demonstrated when the two hemispheres were trained to make opposite choices. The animal was



EFFECT OF BRAIN DIVISION is tested on animals trained to perform a variety of tasks in response to visual or tactile cues. In this test designed by the author the monkey must pull one or the other of two levers with differently shaped handles.

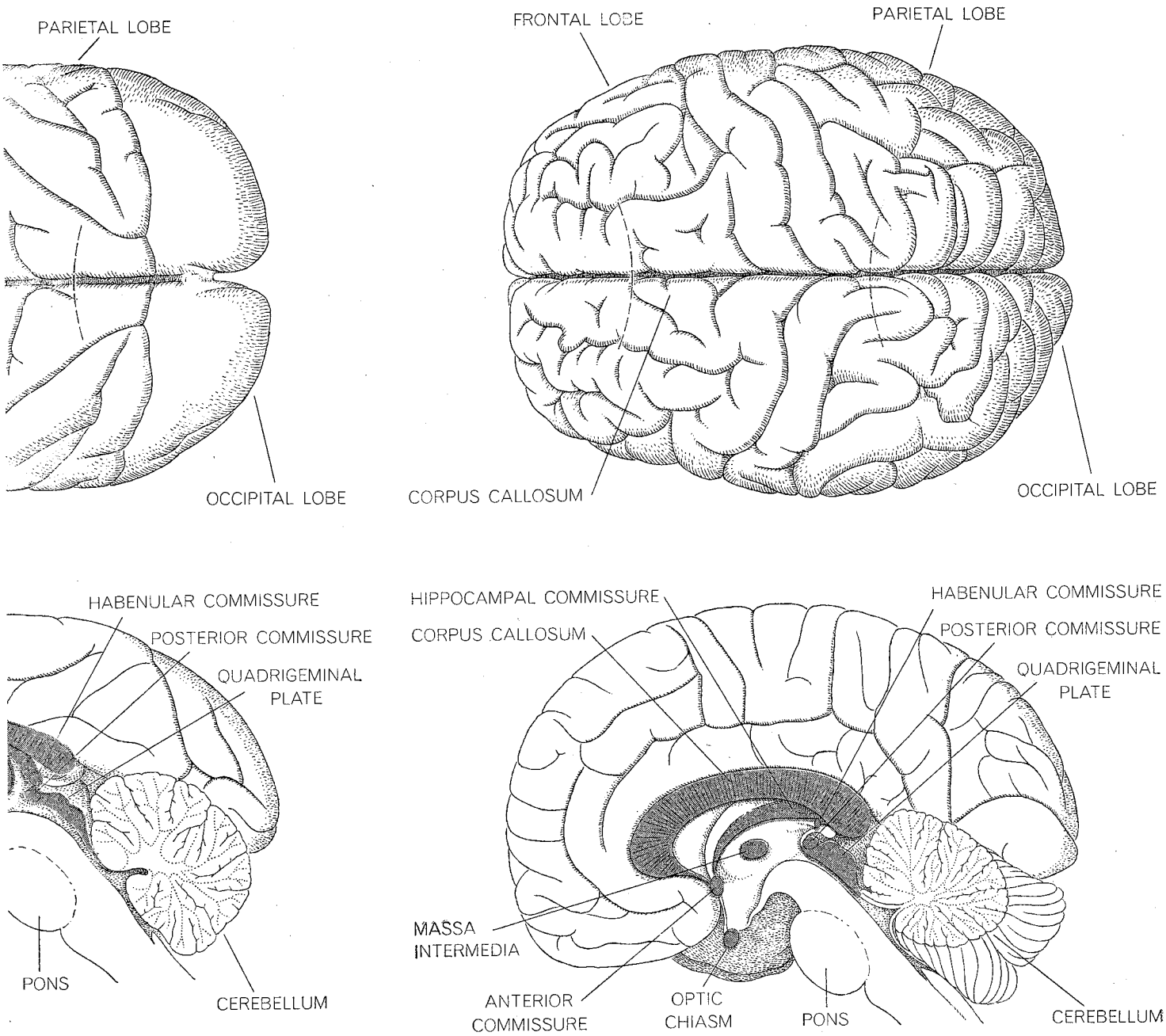


CORPUS CALLOSUM and the other commissures connect the two halves of the mammalian brain. The drawings on these two pages show the brains of a cat (*left*), a monkey (*center*) and a human being (*right*). In each case the top drawing shows the top of the

first trained to choose the square when the pair of symbols was seen through one eye. After learning was complete the eye patch was shifted and the animal was taught with the other eye to reject the square and pick the circle. This reversed training through the separate eyes gave rise to no sign of interference or conflict, as it does in an animal with an intact corpus callosum.

Subsequent studies, many dealing with forms of learning other than the visual–discrimination by touch, motor learning and so on–support the same conclusion. For example, in a special training box in which the animals could not see what their forepaws were doing, John S. Stamm and I trained cats to get food by using a paw to choose correctly between a hard pedal and a soft one, or a rough pedal and a smooth one, or two pedals of different shapes [*see illustration on page 47*]. With the corpus callosum intact, an animal trained to use one paw is generally able to carry out the learned performance when it is made to use the untrained paw; normally the training transfers from one side to the other. But when the corpus callosum has been cut beforehand, the training of one paw does not help the other; on shifting from the first paw to the second the cat has to learn discrimination by touch all over again. The same applies to the learning of a motor task, such as the pattern of finger or paw movements necessary to push a lever or open the hasp and cover of a food well. What is learned with one hand or paw fails, as a rule, to carry over to the other when the corpus callosum has been severed, be it in a cat, a monkey, a chimpanzee or a man.

In short, it appears from the accumulated evidence that learning in one hemisphere is usually inaccessible to the other hemisphere if the commissures between the hemispheres are missing. This means that the corpus callosum has the important function of allowing the two hemispheres to share learning and

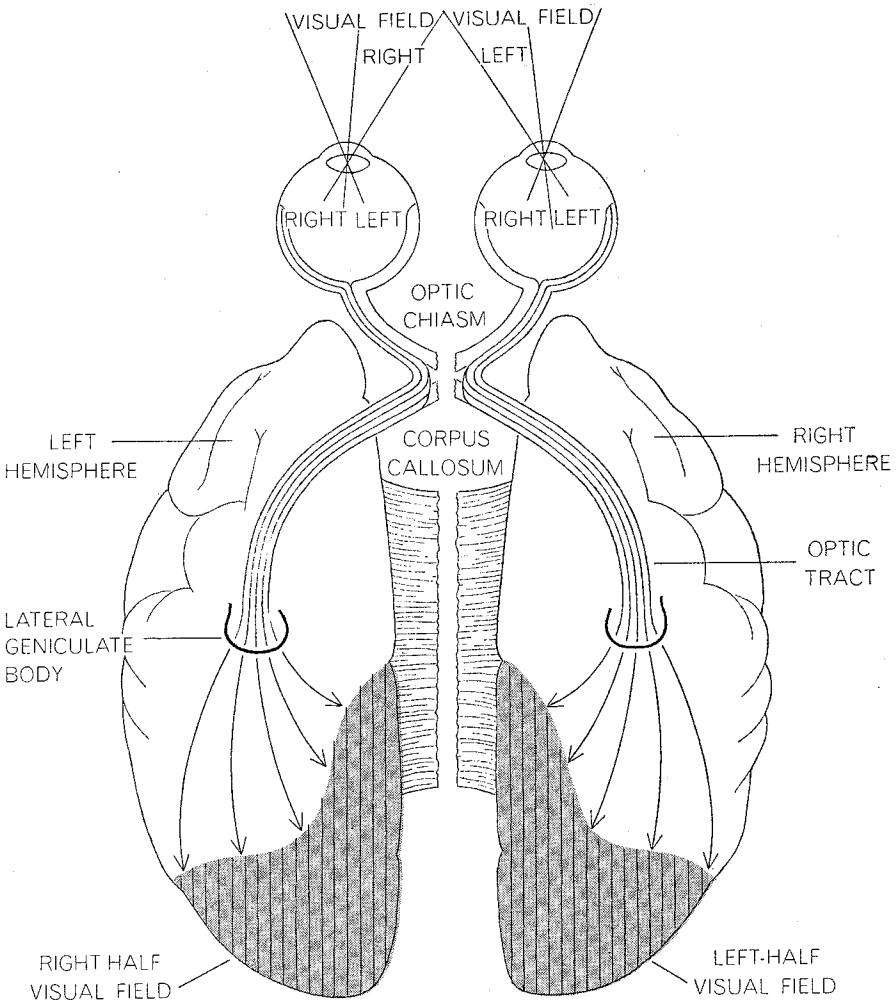


cerebral hemispheres, with the position of the corpus callosum indicated in color. The bottom drawings are sectional views of the right half of the brain as seen from the mid-line; the connecting structures cut in split-brain investigations are designated in color.

memory. It can do this in either of two ways: by transmitting the information at the time the learning takes place, or by supplying it on demand later. In the first case the engrams, or memory traces, of what is learned are laid down both in the directly trained hemisphere and, by way of the corpus callosum, in the other hemisphere as well. In other words, intercommunication via the corpus callosum at the time of learning results in the formation of a double set of memory traces, one in each half of the brain. In the second case a set of engrams is established only in the directly trained half, but this information is available to the other hemisphere, when it is required, by way of the corpus callosum.

By cutting the corpus callosum after learning, and by other methods of investigation, it is possible to determine which of these two memory systems is used in different learning situations and in different species. It appears from present evidence that the cat tends to form engrams in both hemispheres when it is learning something. In man, where one hemisphere is nearly always dominant, the single-engram system tends to prevail, particularly in all memory relating to language. The monkey seems to fall somewhere in between. It sometimes uses the double-engram system, but under other conditions it may lay down engrams in only one of its hemispheres.

Thanks to a wide variety of experiments with cats and monkeys, involving one-side training and testing of various eye-limb and other combinations, we are now beginning to get a fairly detailed picture of the functions of the corpus callosum. It is needed for correlating images in the left and right halves of the visual field; for integrating sensations from paired limbs, or for learning that requires motor co-ordination of the limbs; for unifying the cerebral processes of attention and awareness, and for a number of other specific activities that involve direct interaction of the hemispheres. Furthermore, the corpus callosum seems



VISUAL FIELDS and the visual centers of the brain are related as shown in this diagram of the monkey brain. Cutting optic chiasm and corpus callosum leaves each eye feeding information to one side of the brain only and eliminates the normal overlap of visual fields.

to play important roles of a more general nature. Its absence slows down the rate of learning, at least in some situations. And, like other large nerve-fiber tracts, it has a general tonic effect on the brain cells to which it feeds impulses.

Many of these findings in animals have been checked and confirmed recently in studies conducted on a human patient in whom the hemispheres were surgically separated in an effort to control intractable epileptic convulsions. The seizures had been building up for 10 years in this man after a brain injury sustained in World War II. Philip J. Vogel and Joseph E. Bogen, surgeons at the Institute of Nervous Diseases of Loma Linda University in Los Angeles, cut through the corpus callosum and other commissures. The operation was remarkably successful in ending the attacks. Moreover, the patient, a 49-year-old man above average in intelligence, was left without any gross changes in his personality or level of intellect. In the months after the operation he commented repeatedly that he felt much better than he had in many years. In casual conversation over a cup of coffee and a cigarette one would hardly suspect that there was anything at all unusual about him.

With the collaboration of the patient and his physician, Michael S. Gazzaniga of our laboratory has carried out a series of careful tests probing the man's performances with one or both sides of the brain and body. Like most people, the patient is right-handed, and his dominant cerebral hemisphere is the left one. He is able to perform quite normally most activities involving only the left brain and right side of the body. For example, he can easily read material in the right half of his visual field, name and locate objects in that half, execute commands with his right hand or foot and so on. He does, however, have certain difficulties with activities on his left side.

Up to a point the left side of his body can function normally: he appears to see clearly in the left half of his visual field and has good sensitivity to touch and good motor function on his left side. But in any task that requires judgment or interpretation based on language, which is stored only in his left cerebral hemisphere, he clearly shows the effects of the cerebral disconnection. He cannot read any material that falls in the left half of his visual field, so that when he reads with full vision he has difficulty and tires easily. Nor can he write anything at all meaningful with his left hand. As a rule he cannot carry out verbal commands with his left hand or left leg. When an object is presented solely in the left half of his visual field, he may react to it appropriately but he cannot name or describe it. The same is true of an object placed in his left hand when he is blindfolded. While blindfolded he is unable to say where he has been touched on the left side of the body or to describe the position or movements of his own left hand. In fact, if the dominant hemisphere of his brain is occupied with a task, anything happening to the left side of his body may go completely unnoticed. When his dominant left hemisphere is questioned about nonverbal activities that have just been carried out successfully by the left hand via the right hemisphere, it cannot recall them; this is often the case even when both of his eyes have been open and their visual fields unrestricted. Evidently the dominant hemisphere of the brain neither knows nor remembers anything about the experiences and activities of the other hemisphere.

The separation of the two hemispheres is further indicated by certain specific tests. For instance, when the skin on one side of the subject's body is lightly tapped with the point of a pencil, he can locate the point touched with the hand on that side but not with the other hand. When a spot of light is flashed on a screen in one half of the patient's visual field, he can point to it only with the hand on the same side. In generalized motor activities his left hand usually co-operates with the right, but not always. At times the left hand may go off in a distracted way on independent and even antagonistic activities of its own, which can be troublesome.

These findings are generally confirmed in work begun with a second patient who has more recently recovered from the same kind of brain operation. The results in this individual are not complicated by an earlier brain injury, and two months after the operation the overall recovery picture is even better than it was for the first patient. In particular,

motor control of the left hand is not so markedly impaired.

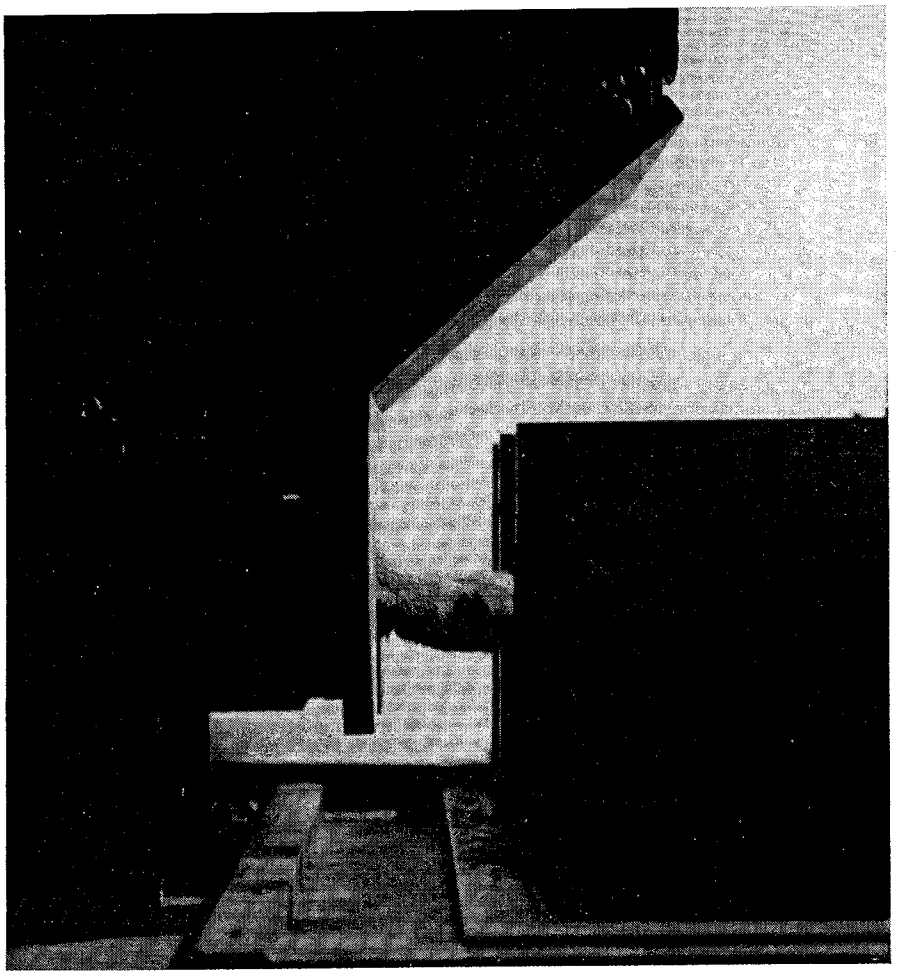
It should be noted again that most of the impairments of brain function from such surgery do not show up in the common activities of daily life. They are detected only under special testing conditions, such as blindfolding the subject, restricting his movements to one or the other hand, using quick-flash projection to confine vision to half of the visual field and so on. One can hope that where the impairments do cause difficulty in ordinary activities, they will be correctible by re-education and other measures as further investigation adds to our understanding of the properties and capacities of the bisected brain.

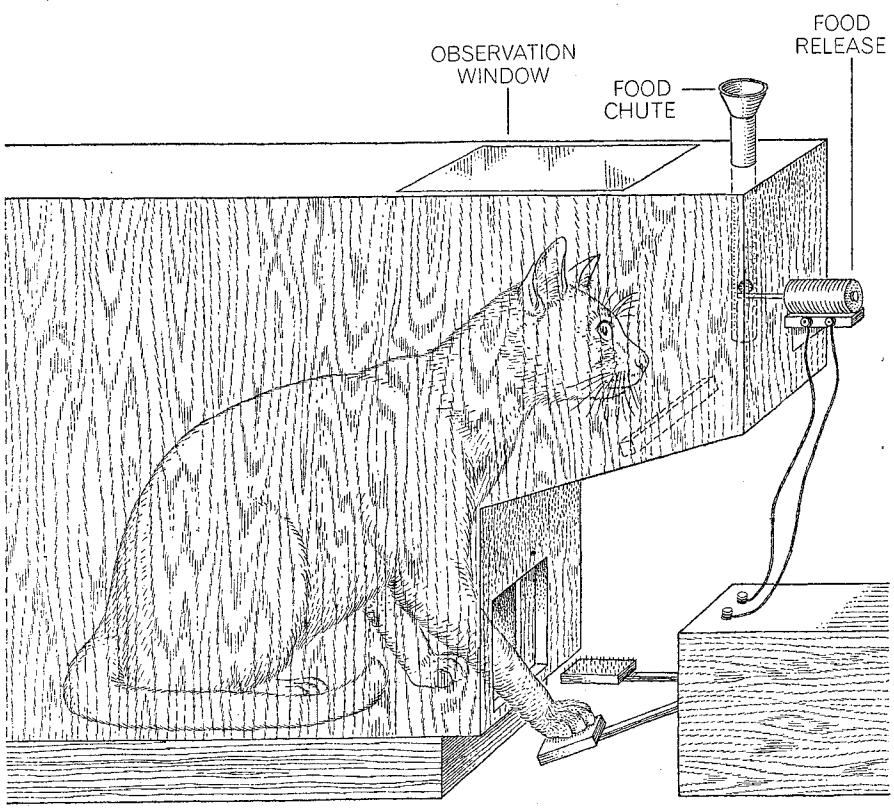
In any case, it is now clear that the loss of the commissural connections between the two halves of the cerebrum does have important and well-marked effects on the functioning of the brain. If the corpus callosum fails to develop at all because of some congenital accident, centers for language and other functions may develop in compensation on both sides of the brain. This seems to have occurred in a nine-year-old boy lacking a corpus callosum, whom we recently tested. As in some earlier cases in the medical literature, he shows almost none of the impairments we observe in the two adult patients.

In other older cases distinct impairments were observed, but they were ascribed to damage in brain areas near the corpus callosum. In the light of present knowledge these cases reinforce the view that damage to the corpus callosum interferes with normal functioning in a number of clearly defined ways. For example, Norman Geschwind of the Veterans Administration Hospital in Boston has recently noted that a patient with a damaged corpus callosum, and similar individuals in the medical literature, have shown effects such as word-blindness, word-deafness and faulty communication between the right and left hands.

Once the enigma of the great cerebral commissure was cleared up and it was firmly established that the commissure really does serve important communication purposes, our interest shifted to more general questions that might be explored by investigation of the bisected brain. Such a brain offered an extraordinary opportunity to examine the many functions and interrelations of parts of the brain, structure by structure and control center by control center.

Bisection of the brain leaves each hemisphere virtually undisturbed. Each





TACTILE DISCRIMINATION is tested with the apparatus shown in the photograph (*top*) and in the diagram (*bottom*). The animal is trained to distinguish between two pedals with different shapes or surface textures. In a normal cat, whatever is learned with one paw is transferred to the other one. But in a split-brain animal each side must learn a task anew.

ization, the inflow of sensory messages and the outflow of motor commands. Each retains its full set of cerebral control centers and the potentiality for performing nearly all the functions of a whole brain. Even the human brain, in spite of the normal dominance of one side, can adapt itself to carry on fairly well when one hemisphere is eliminated early in life because of a tumor or an injury. A monkey with one cerebral hemisphere removed gets along better than a man in a comparable condition, and a cat does much better than a monkey.

Because of the independence of the two halves of the bisected brain, it is possible to study nearly all brain functions by concentrating on one half while the animal carries on normally with the other half. The situation affords certain uniquely helpful experimental conditions. Since the experiments are performed with one hemisphere, the identical opposite hemisphere can serve as a

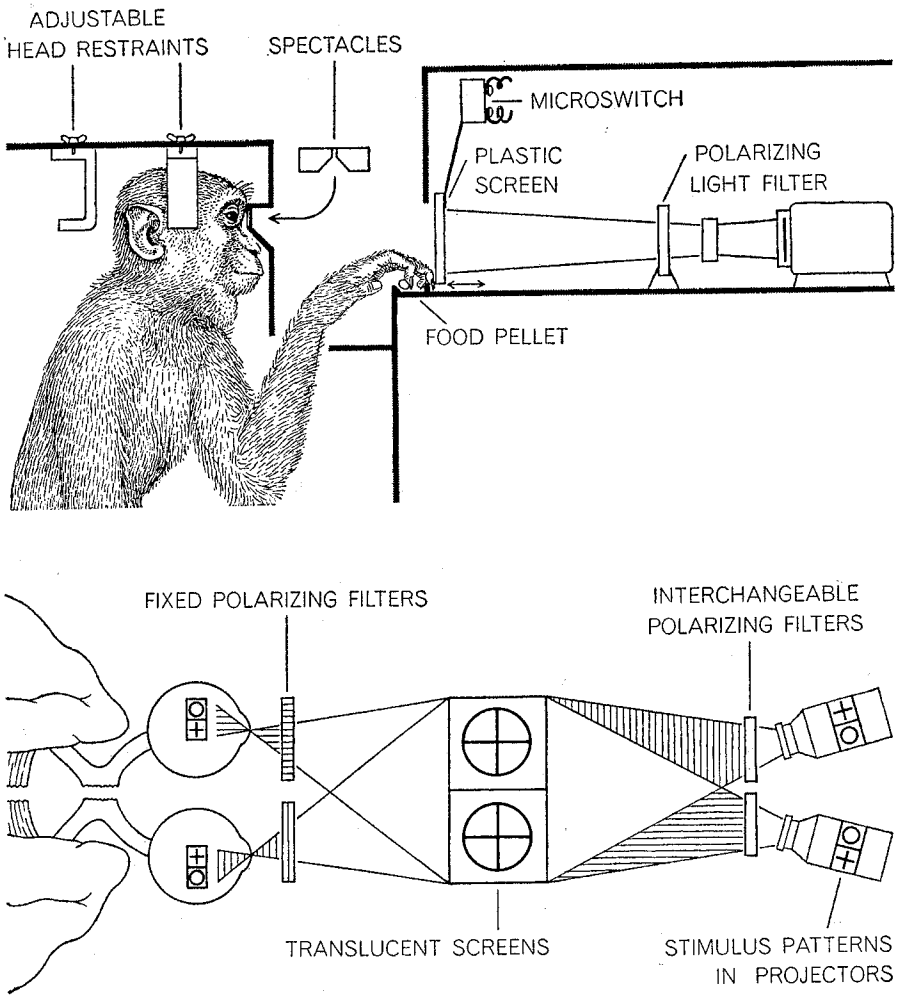
over, the fact that one half of the brain suffices to deal with the animal's needs makes it possible to remove or isolate parts of the experimental half, without disabling aftereffects to the animal, in order to identify the functions of each part.

A first question to arise in this connection is: How far can the brain be divided without grossly disrupting brain-mediated processes? We have already noted that cutting the cerebral commissures does not seriously interfere with the functioning of the two hemispheres. In monkeys the bisection has been carried down through the roof of the brain stem and completely through the cerebellum, leaving intact for cross communication only the tegmentum, or floor of the brain stem [*see illustration on opposite page*]. Such monkeys show some motor unsteadiness, weakness and uncertainty, but they eventually recover their strength and stability. Deeper splits through the tegmentum into the upper

cat by Theodore Voneida of our laboratory. A curious blindness ensued, but it cleared up after several weeks and the animals made a good recovery. The effects on learning and perception of these deepest bisections have not yet been studied in detail. In general, however, it can be said that the two halves of the brain function well even when they are divided down into the upper regions of the brain stem, provided that only cross connections are cut.

The effect on behavior of severing the cross connections between the two halves of the brain is not always simple and unambiguous. An animal with a split brain sometimes behaves as if the two hemispheres were still in direct communication in one way or another. Some of these cases can be explained without difficulty; others are puzzling and call for further investigation.

One case involved the ability to respond to differences in the brightness of light. Thomas H. Meikle and Jeri A. Sechzer of the University of Pennsylvania School of Medicine trained cats to discriminate between brightness differences seen with one eye and then tested them with the other eye. With the corpus callosum severed the cats were able to transfer this learning from one hemisphere to the other when the brightness distinctions were easy to make, but not when they were fairly difficult. The transfer disappeared, however, when cross connections in the midbrain, as well as the corpus callosum, were cut. This case therefore appears to be explainable on the basis that in the cat the process involved is simple enough to occur at a level lower than the corpus callosum. In the monkey and in man, however, the corpus callosum seems to be required for the transfer of even the simplest brightness or color discrimination.



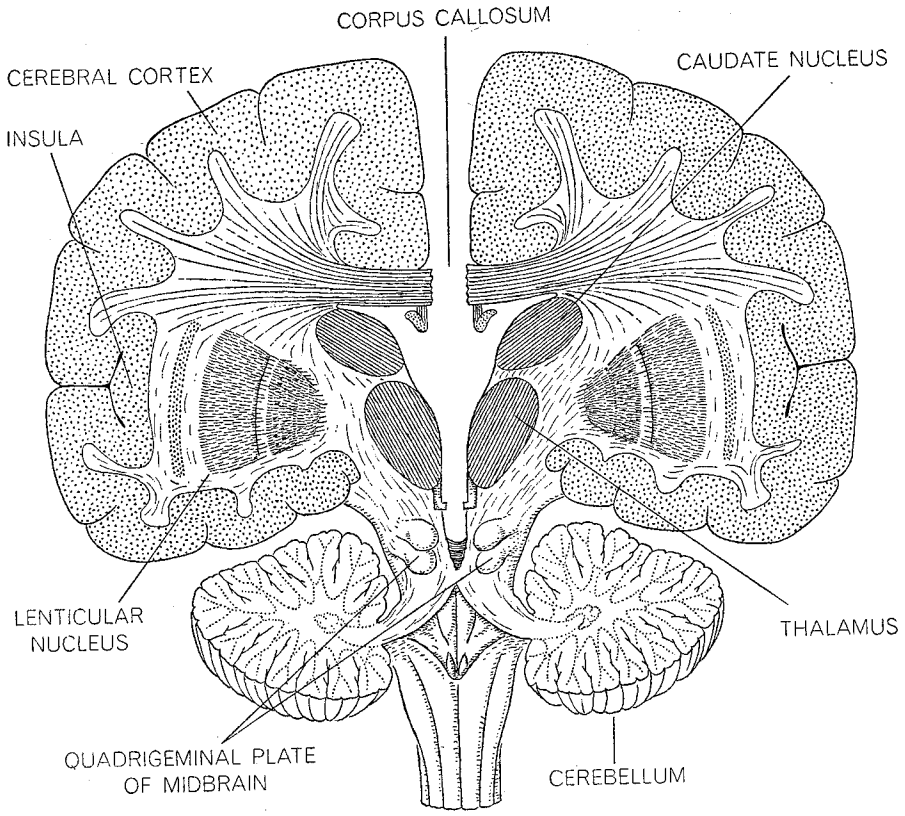
PERCEPTUAL CONFLICT in split-brain monkeys is tested with the apparatus shown in the top drawing. It presents a different image to each eye, as seen in the bottom diagram. While one of the animal's isolated eye-brain systems learns that pushing the panel with the cross is rewarded by food, the other eye-brain system learns to push the circle instead.

There are types of cross communication that can take place in a split brain because both sides of the brain are directly connected to the motor system or sensory organ involved. For example, each brain hemisphere receives sensory messages from both the right and the left sides of the face and other parts of the head; consequently the separation of the hemispheres does not interrupt the communication of sensations between the two sides of the head. Hearing in each ear is likewise extensively represented in both cerebral hemispheres. The same may apply in lesser degree to certain sensations in the limbs and the rest of the body; this may explain why learning involving hand and arm movements in monkeys

with split brains may on occasion transfer from one side to the other.

There is also the possibility of indirect communication between the split halves of the brain through feedback from activity in the body. A motor activity directed from one hemisphere may involve widespread bodily movements that will feed back messages to the opposite hemisphere as well as the active one. For instance, an action performed by one hand is likely to involve adjustments in posture and muscular activity that spread to the other side of the body and thus make themselves known to the other hemisphere. Unifying factors of this sort help to account for the fact that the two sides of the body do not act more independently in a split-brain situation. They do not, however, change the general inference that the two brain hemispheres are for the most part separate realms of knowledge and awareness.

A special case of cross transfer that was at first quite surprising was discovered recently in our laboratory by Joseph Bossom and Charles R. Hamilton. Their experiments dealt with the way in which the brain adjusts itself to overcome the distortions produced by looking through a wedge prism. Such a prism so displaces the visual scene that in reaching for an object the hand misses its mark. With a little practice, however, the eye-brain system soon achieves the necessary corrections to hit the target every time. Bossom and Hamilton trained split-brain monkeys to adapt themselves to the problem using one eye. After the monkeys had learned to correct for the displacement of the prism, they were switched to using the other eye. The learning was fully and immediately transferred—even in monkeys with a deep bisection through the brain-stem roof and cerebellum. This seemed to contradict the earlier experiments showing a lack of transfer of learning from one eye to the other. But when Hamilton followed up with repetitions of the experiments in which the monkey was made to practice the prism adaptation using only one hand, he found that corrective adjustments achieved through the one hand, in combination with either eye, do not transfer to the other hand. This suggested that the central adjustment to deflections of a target by a prism depends primarily on the brain centers concerned with motor activity and bodily sensations rather than on those involved in vision. This interpretation has now been supported in an extension of the study to human subjects. It is still not clear, however, how split-brain monkeys achieve this adjustment so easily when the visual inflow is confined to one hemisphere and the only hand in use is the one governed primarily from the other hemisphere.

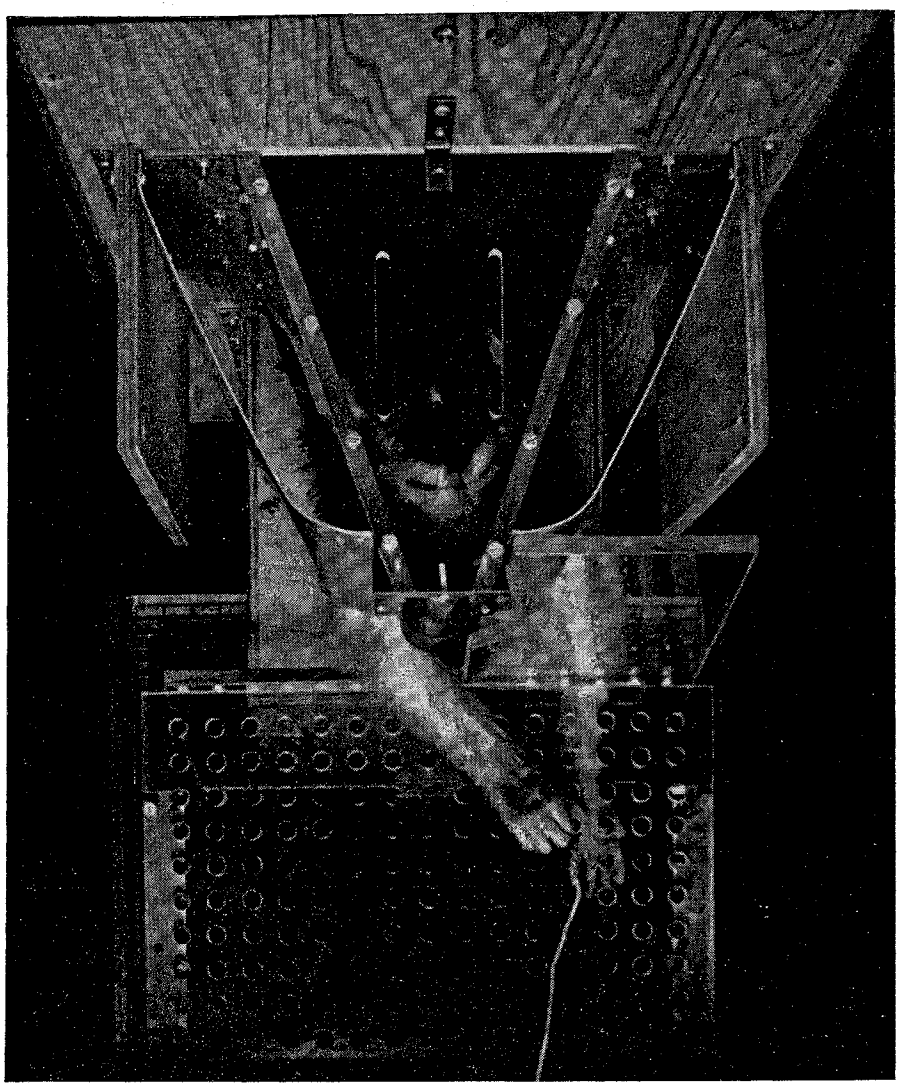


DEGREE OF SEPARATION among the higher brain centers that is produced by the surgical procedures discussed by the author is shown in this semisectional diagram of the brain.

Certain other performances under study in our laboratory that appear to involve cross integration in the divided brain are even harder to explain. For example, Colwyn B. Trevarthen and I have found that a split-brain monkey can learn to select the larger (or smaller, as the case may be) of two circles of different sizes presented separately to the two brain hemispheres, the larger to one and the smaller to the other. To make the *relative* size count, the circles are selected from a series of five graded sizes. It would seem that to make the comparison successfully the two hemispheres, although cut apart, must collaborate in some way. Similarly, I have found that split-brain monkeys grasping two handles separately, one in each hand, can pick the larger or the rougher of the pair. Here again five different sizes and five degrees of roughness are paired in random right-left position.

Difficult as it is to avoid the conclusion that the two brain hemispheres are working together in these cases, the strong evidence of many experiments on the independence of the divided hemispheres suggests that one should seek other explanations. It is conceivable, for example, that a combination of independent strategies used by the two hemispheres might have produced a high score without any real exchange of information. The discrimination of handles by touch might have been aided by cross communication through related sensations of movement or from motor feedback. It is also possible that the apparent communication between the hemispheres may have been achieved by way of interactions taking place in the lower brain stem or even in the spinal cord. These and other possibilities are being investigated.

Another group of observations revealed an interesting and significant difference between animal and human brains. The tests had to do with the ability of one side of the body to respond to visual cues received only by the cerebral hemisphere that directs the opposite side of the body. For example, with the corpus callosum divided and with vision restricted to one hemisphere, the animal is trained to reach out and pick by vision the correct one of two objects; can the subject do this when allowed to use only the hand or paw that normally is associated with the unseeing hemisphere? The cat proved to be able to use either forepaw under these conditions with about equal ease. The monkey does not



HAND-TO-HAND CO-ORDINATION is tested in this experiment. The split-brain monkey cannot see the plastic divider that prevents contact between its hands. By groping, it finds a peanut with its upper hand. It can retrieve the peanut only by poking it down through a hole and catching it with its lower hand. The only cues it has for placing the lower hand are based on a joint-and-muscle sense of the position and movement of the upper hand.

do so well; sometimes it can co-ordinate its motor response with the visual message and sometimes not. In human patients, on the other hand, this ability is severely disrupted by the severing of the corpus callosum. As we have already noted, in the split-brain patient who was extensively tested the left hand generally is unable to respond correctly to commands or visual stimuli presented only to the left cerebral hemisphere. The patient without prior brain injury does somewhat better, but even so the performance is markedly poorer than that of the monkey.

The same applies to stimuli of other kinds. For instance, when the human patients are blindfolded and hold a pencil in one hand, the other hand is unable to find the end of the pencil if the hand holding the pencil shifts its angle or changes its position in some other way. When monkeys whose corpus callosum had been cut were put to similar tests by Richard F. Mark and me, however, they performed almost normally [*see illustration above*]. And when all the cross connections down through the roof plate of the midbrain, with the exception of the corpus callosum, were cut, the performance also went well. Subsequent cutting of the corpus callosum in this last situation finally abolishes the performance, showing the participation of the corpus callosum. Even so, the difference between man and monkey in the expendability of the corpus callosum for such hand-to-hand activities remains striking.

Here we are probably seeing a reflection of the evolution of the brain. The appearance and development of the corpus callosum in evolution parallels the appearance and development of the cerebral cortex. As in the course of evolution central controls are shifted from more primitive brain-stem areas to higher stations in the ballooning cerebral cortex, the role of the corpus callosum becomes more and more critical. So also do the phenomena of dominance and specialization in the hemispheres of the cerebrum. In cats and lower animals the two hemispheres seem to be essentially symmetrical, each learning equally and each capable of serving by itself almost as a whole brain. In the monkey the two hemispheres are apparently somewhat more specialized. As the accumulation of memories, or the storage of information, becomes more important in the higher animals, the duplication of memory files in the two brain hemispheres is given up for a more efficient system: the division of labor by the assignment of specialized files and functions to each hemisphere. This evolution has culminated in the human brain. Here a distinct separation of functions prevails: language is the task of the dominant hemisphere and lesser tasks are largely taken over by the other hemisphere.

The question of dominance is crucial for the effective functioning of the brain as the master control system. Bear in mind that the brain is composed of twin hemispheres, with a full set of control centers in each hemisphere that enables it to take command and govern the general behavior of the animal. What happens, then, if the two halves of an animal's split brain are taught to give completely conflicting responses to a given situation?

The devices developed in our laboratory allow a great variety of experiments, using all sorts of combinations of brain control centers with the sensory and motor organs of the body. They can restrict the animal to the use of one eye or the other with one hand or the other, to the tactile sense without vision, to vision in one brain hemisphere and the tactile sense in the other, and so on. A representative apparatus for the monkey, designed for experiments involving visual stimuli and responses with the hand, is shown in the illustration on page 43. The monkey stations itself behind a barrier that can be adjusted to let it see with both eyes or the right eye or the left eye or neither, and to let it use both hands or only the right or the left. By the use of light-polarizing filters, the visual stimulus (for example a circle) can be split and the two images projected separately to the two halves of its visual field in order to determine if the subject can integrate them. The monkey's responses consist in pressing buttons, pulling levers

and so forth; these responses are rewarded when they are correct. We can hook up to this apparatus automatic equipment that is programed to present any of a number of different problems to the animal. In that case the apparatus is attached to its home cage as a kind of porch where the monkey can station itself as the spirit moves it and work at its leisure.

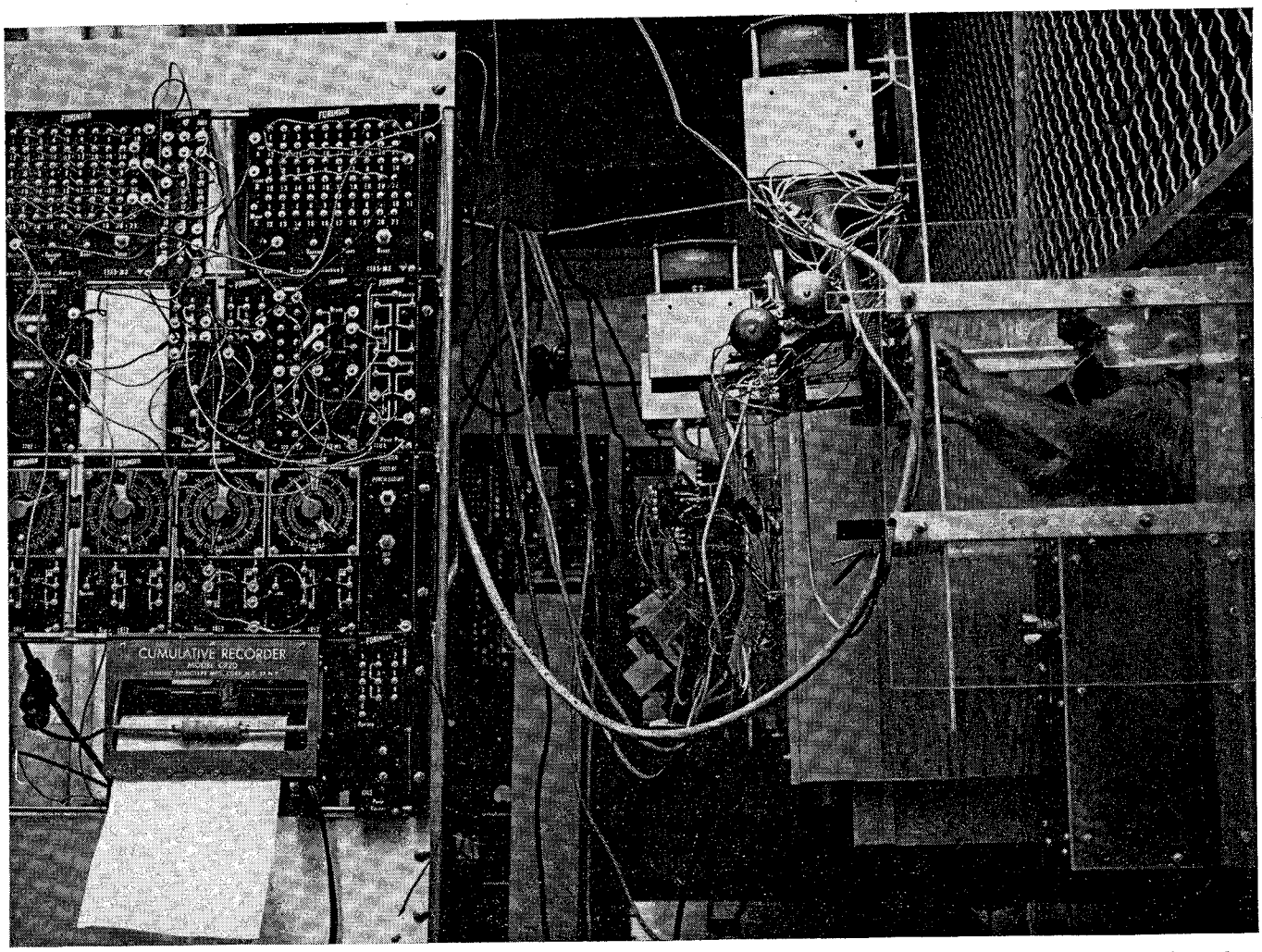
With this apparatus a split-brain monkey can be trained, let us say, to choose between a triangle and a square as the rewarding stimulus. Looking through its left eye, it learns to select the triangle as the reward; through the right eye, the square. It is trained for a few trials with the left eye, then for a few trials with the right, and this alternation is continued until each eye comes to give a nearly perfect performance, even though the responses with the separate eyes are contradicting each other. As we have already noted, the animal usually evinces no conflict in this paradoxical situation: the left eye unhesitatingly chooses the triangle and the right eye the square. Here the split-brain monkey learns, remembers and performs as if it were two different individuals, its identity depending on which hemisphere it happens to be using at the moment.

What if the two hemispheres are asked to learn these mutually contradictory answers simultaneously instead of one at a time alternately? Can each hemisphere attend to its own lesson and file one answer in its memory while the other is filing a conflicting answer in *its* memory?

Trevarthen found a way to investigate this question by introducing polarizing filters to present reversed pictures simultaneously to a monkey with both eyes open [*see illustration on page 48*]. A pair of patterns (say a cross and a circle, but any pair of patterns or colors will do) is projected separately to the two eyes. To one eye it appears that the food reward is won by pushing the cross; to the other eye it seems that the circle is being pushed. In other words, for one hemisphere the correct answer is "cross" and for the other it is "circle," but the panel that is pushed is the same in both cases. After the monkey, using both eyes, has learned to push the correct panel 90 per cent of the time, it is tested with each eye separately.

It turns out that there is a strong tendency for one hemisphere (usually the one governing the arm that is first used to push the panels) to learn the answer sooner and more fully than the other. This suggests that active attention by one hemisphere tends to weaken the attention of the second, although the activities of the two have no direct connection. Trevarthen has found, however, that sometimes both hemispheres learn their respective answers fully and simultaneously. That is, the split-brain monkey in these cases divides its attention between the two hemispheres, so that it masters the two contradictory problems in about the same time that a normal, single-minded monkey would be learning one problem.

This doubling of attention is also manifest in Gazzaniga's tests on the split-



AUTOMATED EQUIPMENT is adapted to tabulating and recording the data from a number of trials conducted with several monkeys over a period of time. The animals work at their tasks at their leisure, moving to apparatus affixed to the rear of their cages.

brain human patient discussed earlier. The test consisted in asking the man to pick a certain figure out of a pair of figures flashed very briefly (for less than a tenth of a second) and simultaneously in each of his visual fields—one pair in the left field and one pair in the right. The subject abruptly points to the correct figure in the left field with his left hand (governed by the nondominant hemisphere) and at the same time indicates the correct figure in the right field verbally or by pointing (this act being governed by the dominant hemisphere, which controls language and speech). Discussing such responses afterward, the patient typically has no recollection of having pointed with his left hand; the dominant hemisphere seems completely ignorant of what went on in the other one.

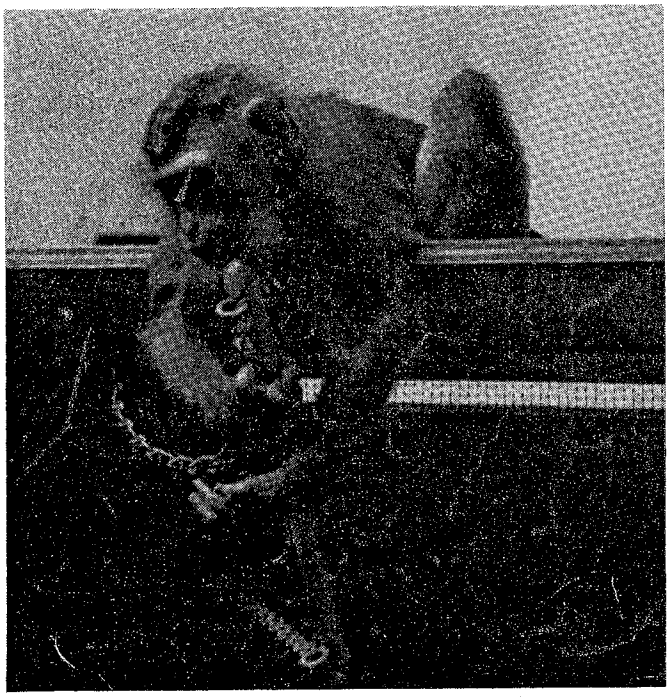
These remarkable indications of a doubling of the psychic machinery in the brain raise a number of new questions about the roles played in the learning process by attention, perception and motivation. There are also many intriguing philosophical implications. When the brain is bisected, we see two separate "selves"—essentially a divided organism with two mental units, each with its own memories and its own will—competing for control over the organism. One is tempted to speculate on whether or not the normally intact brain is sometimes subject to conflicts that are attributable to the brain's double structure.

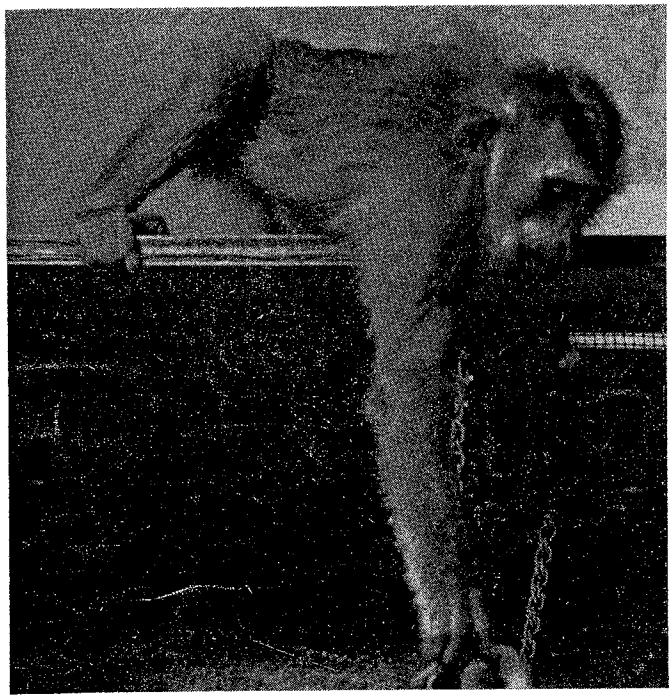
How does an animal with a split brain resolve the dilemma of being conditioned to two directly opposite answers to a given problem? Suppose it is confronted with a situation in which it must make a choice between two "correct" answers? Can it master the conflict, or is it paralyzed like the proverbial donkey between a bag of oats and a bale of hay?

The kind of answer that is usually obtained is illustrated in an extension of the experiment with polarizing filters. After the split-brain monkey has been trained so that one hemisphere considers as correct the panel marked by a cross and the other hemisphere considers as correct the panel marked by a circle, one of the eye filters is turned 90 degrees. Now instead of the images being reversed in the two eyes, both eyes see the pair of symbols in the same way—say the cross on the left and the circle on the right. Will the animal, with both eyes open, choose the cross or the circle or waver in confusion between the two? In such tests the monkeys, after only a little indecision and hesitation, make a choice and adhere to it: they consistently select the cross or the circle for a series of trials. That is, one hemisphere or the other takes command and governs the monkey's behavior. This dominance may shift from time to time, each hemisphere taking its turn at control, but it would appear that no serious conflict disrupts any given movement.

Something more akin to conflict between the separated hemispheres is occasionally seen in tests given the human patients. Incorrect responses by the left hand may so exasperate the more sophisticated dominant hemisphere that it reaches across with the right hand to grab the left and force it to make the correct choice. Or conversely, when the literate hemisphere and right hand fail in a block-arrangement test—one of the few things that the left hand and nondominant hemisphere generally do better—impatient twitches and starts occur in the left arm, which may have to be restrained to keep it from intercepting the right. As in split-brain cats and monkeys, however, one hemisphere or the other generally prevails at any given time. Any incompatible messages coming down from the other hemisphere must be inhibited or disregarded.

The experiments discussed in this article are a sample of the large variety of studies with the split brain that are being carried on by our group at Cal Tech and by others in laboratories elsewhere. Work with the split brain has enabled us to pinpoint various centers of specific brain activity, has suggested new concepts and new lines of thought and has opened up a wealth of new possibilities for investigating the mysteries of the mind.





RHESUS MONKEYS whose brains have been bisected perform well in most general play and exercise tests. These animals with split brains are hardly distinguishable from normal monkeys in their ability to move about, find and retrieve food and do acrobatics.